ROOT:SHOOT BIOMASS RATIOS IN SHRUBS IN SOUTHERN CALIFORNIA AND CENTRAL CHILE

PHILIP C. MILLER AND EDWARD NG[1]

Department of Biology
San Diego State University, San Diego, CA 92182

One characteristic of vegetation in mediterranean-type climates is an abundance of deep-rooted shrubs (Hellmers et al., 1955; Sacchori et al., 1967). The deep rooting patterns correspond with the cool, wet winter and hot, dry summer climatic pattern in which water is available deep in the soil when surface layers are dry and temperatures are favorable for photosynthesis and growth (Miller and Mooney, 1974). Where evergreen, sclerophyllous shrubs predominate, annual precipitation is about 400–650 mm (Aschmann, 1973; Miller et al., 1977). Deep rooting patterns imply an investment of carbon resources by the plants in the root system, but there are few data on the root:shoot biomass ratios for shrubs in mediterranean regions, probably because of the difficulty in obtaining these figures (Kummerow et al., pers. comm.). At the beginning of this study we expected to find that root-shoot biomass ratios of shrubs in the mediterranean climatic regions of southern California and central Chile would be greater than one and that the biomass of absorbing roots, identified by small root size, would be correlated with the transpiring leaf area of the shrub. Our field study tested these hypotheses on selected shrubs in the 2 regions. We excavated 14 individual shrubs of 6 species: 8 in southern California and 6 in Chile. The main comparison involved 2 Californian species: *Adenostoma fasciculatum* (4 shrubs excavated) and *Ceanothus greggii* (2 shrubs excavated); and 2 species of similar areal stature in Chile, *Satureja gilliesii* (4 shrubs) and *Colliguaya odorifera* (2 shrubs). In addition, one plant of *Heteromeles arbutifolia* and one of *Arctostaphylos glauca* were excavated in California.

DESCRIPTION OF STUDY SITES

In California roots of all plants except the *Heteromeles* and one *Adenostoma* (*Adenostoma* 4) were excavated at Echo Valley in San Diego County (32°54′N, 116°39′W). These 2 plants were excavated near the Viejas Road, 15 km southwest of the Echo Valley site. In Chile all the plants were obtained by excavating back from a road cut at the Fundo Santa Laura site (33°04′S, 71°00′W). We used hydraulic excavation to remove roots from the soil. This requires large volumes of water, a high pressure pump, and suitable drainage away from the root washing site. Rapid drainage of water and soil was necessary during excavation

[1]Present address: Department of Agronomy, University of California, Davis 95616

to keep the root system exposed and allow its extraction. Therefore, plants near road cuts or on steep banks were chosen. However, the center of the excavated plant was always more than 1 m from the road cut. Roots were excavated at comparable sites in California and Chile: approximately 55 km from the coast at about 1,000 m. Annual precipitation in both regions is about 550 mm, with about 60% during the winter 6 months in California and 83% in the analogous months in Chile (Miller et al., 1976). The annual mean temperatures at the research sites are about 17C in California and 15C in Chile. The Californian site burned in 1950. The Chilean site was subjected to wood cutting prior to 1959, although the species measured are not used for firewood (Aschmann and Bahre, 1977). Root excavations in both countries were made during the respective summer when surface layers of soil were dry but subsurface layers were still moist. Roots were excavated in June, July, and August, 1971 in California and in February, 1972 in Chile. Precipitation through the winter preceding the excavations was about 250 mm at the site in California. A complete precipitation record prior to excavations is not available in Chile; however, in California there was no precipitation during the 2 months preceding excavations, and in Chile none during the 4 months preceding excavations. Average soil moisture at 0.3–1.2 m depth decreased from 0.25 to 0.09 cm^3 water per cm^3 soil during the excavations in California; thus, the soil was presumed to be dry at excavation in both countries.

Shrubs excavated from the Echo Valley site were growing near recent road cuts; those from the Viejas site were adjacent to recent excavations for land fill. Slope inclinations were 10°–15° for each site. Slope exposure of the plants at Echo Valley was north; *Adenostoma* 4 was on a south–facing, and *Heteromeles* on an east–facing exposure. The soils at both excavation sites are sandy loams, underlain by decomposed granite from weathered Bonsall Tonalite, without much vertical stratification and, although of variable depth, more than 0.5 m deep. The soils at the Viejas site were much rockier than those at Echo Valley. *Ceanothus* and *Adenostoma* were excavated in a mixed stand of these species. *Adenostoma* 4 was in a pure *Adenostoma* stand. *Arctostaphylos* was associated with *Quercus agrifolia* and *Quercus englemanii,* and *Heteromeles* was associated with *Q. agrifolia* and *Salvia apiana*. No herbaceous cover occurred on the plots excavated.

The excavation site in Chile was predominantly northwest facing. The slope inclination was highly variable but was 10°–25° where excavations were made. The surrounding vegetation was dominated by *Satureja gilliesii* and *Colliguaya odorifera,* with occasional *Lithraea caustica, Trevoa trinervis* and *Cryptocarya alba*. The site had a definite herbaceous layer. Soils were generally coarse textured but not underlain by decomposed granite. The absence of decomposed granite facilitated the excavation.

Methods

For hydraulic excavations in California a 400–gal tank truck and a Barnes impeller type pump were used. The pump was capable of putting out 15 gal min^{-1} at 100 lbs in^{-2} pressure. A similar pump configuration was assembled in Chile where two 50–gal drums provided water storage. The relatively low outflow rate was important because the water supply was limited and sites were remote from the source. A variable nozzle regulated the pressure of water from a narrow, high pressure stream to a fine spray. The fine spray minimized loss of root material during excavation, but the narrow high pressure stream was necessary to remove the soil.

For selected plants, maximum height and radial extent of the crown were measured, and the foliage was tied. Three metal reference stakes were placed in the ground, two in the upper and lower edges of the plot 0.5–1.0 m from the plant, and the third as close as possible to the plant, without piercing its burl (lignotuber). The stakes served as depth gauges while washing the soil and to support the plant as it was undercut. As soil was washed away, exposed roots were marked according to depth. Depth was recorded every 0.2 m in California and every 0.1 m in Chile. Excavation stopped when a impenetrable layer of soil or rocks was reached, when the drainage became insufficient because the level of the road was reached, or when the root system was exposed as completely as possible. Maximum radial extent of the root system was measured. The entire plant was then brought into the laboratory and separated by level for oven drying for 24 hr at 85C.

In California, unbiased estimates of the biomasses of different sized roots, total root length, and root area could not be made because of the nature of the excavation. The decomposed granite washed away in 0.5–1.0 cm^3 chucks, which probably contained most of the fine roots. Therefore, only dry weights of all roots in each stratum were measured. In Chile the soil particles disintegrated more readily with the application of water and fewer fine roots were lost. The retention of small roots allowed those of each plant to be divided into size classes of different diameters within different soil depths. The dry weights of roots in each class were measured. Roots were randomly subsampled from similar size classes and their total length and weight were measured to obtain a length:weight ratio for each size class. The length:weight ratio times the weight and diameter were used to estimate the area of each size class of roots.

Results and Discussion

Even with the variable size of shrubs of the same species, the measured root:shoot biomass ratios were less than one for all individuals (Table 1). The largest root:shoot ratio of an individual was 0.93 and the smallest, 0.25. *Ceanothus greggii,* a shallow–rooted species, had the smallest root: shoot ratios (0.25 and 0.39), while *Adenostoma fasciculatum,* a deep–rooted species, had root:shoot ratios of 0.49–0.69. *Heteromeles,* which is

TABLE 1. SUMMARY OF SHRUB SIZE MEASUREMENTS. Diameter, area, and volume refer to the areal extent of the shoot and root systems, not to an individual shoot or root.

	Species and number of individual														
	Ceanothus greggii		*Adenostoma fasciculatum*				*Heteromeles arbutifolia*	*Arctostaphylos glauca*	*Satureja gilliesii*				*Colliguaya odorifera*	
Plant part	1	2	1	2	3	4	1	1	1	2	3	4	1	2
Shoot														
Height (m)	1.10	0.71	0.40	—	0.54	0.95	1.79	1.05	1.00	0.95	0.90	0.85	0.60	0.20
Diameter (m)	0.40	0.35	0.25	—	0.15	0.93	0.75	1.00	0.70	1.25	0.60	0.80	0.32	0.14
Area (m^2)	0.13	0.10	0.05	—	0.018	0.67	0.45	0.78	0.39	1.23	0.28	0.50	0.08	0.015
Volume (m^3)	0.14	0.07	0.012	—	0.001	0.63	0.80	0.82	0.39	1.16	0.25	0.42	0.05	0.003
Biomass (g)	249.0	30.0	17.0	15.0	14.0	506.0**	342.0	215.0	355.0	357.0	67.0	117.0	47.0	7.0
Stem biomass (g)	151.0	18.0	—	—	—	—	263.0	559.0**	—	—	—	—	—	—
Leaf biomass (g)	97.0	12.0	—	—	—	—	79.0	215.0	—	—	—	—	—	—
Root														
Depth (m)	0.3	0.3	0.3	0.8	1.0	1.0	0.3	0.3	0.4	0.6	0.7	0.85	0.3	0.6
Diameter (m)	0.6	0.4	0.3	—	0.4	2.4	0.6	1.2	1.2	2.0	—	1.4	—	—
Area (m^2)	0.28	0.13	0.07	—	0.13	4.52	0.28	1.64	1.64	3.14	1.2*	1.54	—	—
Volume (m^3)	0.085	0.038	0.021	—	0.13	4.52	0.085	0.49	0.63	1.88	0.84	1.30	—	—
Biomass (g)	63.0	11.0	8.4	11.0	9.0	250.0	254.0	670.0**	125.0	260.0	62.0	90.0	28.0	5.0
Mean biomass density ($g\ m^{-3}$)	740.0	290.0	400.0	—	69.0	55.0	3000.0	1370.0	198.0	138.0	74.0	69.0	—	—
Burl														
Biomass (g)	—	—	—	—	—	—	—	—	152.0	207.0	34.0	108.0	11.0	0.0
TOTAL BIOMASS (g)	311.0	41.0	25.0	26.0	23.0	756.0	596.0	1444.0	480.0	617.0	129.0	207.0	75.0	12.0
ROOT:SHOOT BIOMASS RATIO	0.25	0.39	0.50	0.69	0.63	0.49	0.74	0.87	0.35	0.73	0.93	0.77	0.60	0.89

** Includes weight of burl.
* Area was oblong, 2.4 × 0.5 m^2.

considered deep–rooted, and *Arctostaphylos glauca, Satureja,* and *Colliguaya,* which are all considered shallow–rooted, had similar root:shoot ratios, usually 0.60 to 0.93.

Except for *Heteromeles,* the ground surface area underlain by the roots of an individual was larger than the vertical projection of the crown (Table 1) (Hellmers et al., 1955). The ratios of the ground surface underlain by roots to the vertical projection of the crown were: *Ceanothus,* 1.9–2.0; *Adenostoma,* 6.7–7.2 in two deeper-rooted plants and 1.4 in the shallow–rooted plant; *Arctostaphylos,* 2.1; and *Satureja,* 2.6–4.4.

Roots were concentrated in the upper 0.3 m of soil (Table 2). In *Ceanothus, Heteromeles, Arctostaphylos,* and one *Adenostoma* all of the root biomass was in the upper 0.3 m. In the other *Adenostoma,* 50–55% of the biomass was in the upper 0.3 m and over 94% in the upper 0.8 m. Roots of *Adenostoma* extended to at least 1 m on large plants. In *Satureja* 83–100% of the root biomass was in the upper 0.3 m, with maximum root depths between 0.4 and 0.84 m. In *Colliguaya* over 84% of the root biomass was in the upper 0.3 m, with roots of one individual extending to 0.6 m. Rooting depth appeared independent of root weight both within a species and with all species combined, but was directly related to shoot height in *Satureja* and *Colliguaya.* Root biomass densities of 100–1400 g dry weight m^{-3} in the 0–0.3 m depth (Table 3) compare with values for crop plants of 300 g m^{-3} (Penning de Vries, pers. comm.), and tundra plants of 1,000 g m^{-3} (Dennis and Tieszen, 1972). Root biomass densities at the surface were less with deeper–rooted individuals, indicating a trade–off between high exploitation of the surface and exploitation of the deeper soil.

Mean root diameters decreased with depth in *Satureja* and *Colliguaya,* the only species for which root weights could be measured by diameter class (Table 4). At each depth the length of the roots in the smallest diameter class was larger than that for the other diameter classes. Roots smaller than 0.5 mm diameter comprised 10–25% of the total root biomass and 40–50% of the total root length. The weight of the small roots decreased with both shoot and root biomass. Percentage of the total root biomass which was small roots decreased with increasing root biomass because of the increasing diameter of roots with age and did not correlate with the shoot biomass in the measurements.

Our excavation underestimated the root biomass because of the loss of fine roots in excavation (Caldwell and Fernandez, 1975) and because of the death and sloughing of fine roots as the soil dried in early summer, but a correction for this loss does not increase root:shoot ratios greatly. The correction is based on concepts of absorbing root densities required for the absorption of phosphorus, nitrogen, and water. Chaparral soils are generally considered to be nitrogen and phosphorus deficient (Hellmers et al., 1955; Christensen and Muller, 1975) and are dry during the

TABLE 2. PERCENTAGES OF SHOOT BIOMASS AND OF ROOT BIOMASS IN DIFFERENT LEVELS ABOVE AND BELOW THE SOIL SURFACE.

Plant part	Species and number of individual													
	Ceanothus greggii		*Adenostoma fasciculatum*				*Heteromeles arbutifolia*	*Arcto-staphylos glauca*	*Satureja gilliesii*				*Colliguaya odorifera*	
	1	2	1	2	3	4	1	1	1	2	3	4	1	2
Shoot														
1.5–1.8							6							
1.4–1.6							10							
1.2–1.4							5							
1.0–1.2	15						10	1						
0.8–1.0	28					11	9	10	1	1	3	1		
0.6–0.8	26	3				38	12	18	5	9	16	7		
0.4–0.6	10	43		8	22	21	17	19	21	12	17	21	15	
0.2–0.4	11	34	24	54	42	29	13	22	26	17	23	23	30	
0.0–0.2	10	20	76	38	36	*	17	29	47	61	41	48	56	100
Root	**	**	**	***	***	***	**	**						
0.0–0.1	100 (0.0–0.3)	100 (0.0–0.3)	100 (0.0–0.3)	41 (0.0–0.2)	44 (0.0–0.2)	37 (0.0–0.2)	100 (0.0–0.3)	100 (0.0–0.3)	48	49	51	38	68	55
0.1–0.2									28	39	17	24	30	14
0.2–0.3				20 (0.2–0.4)	21 (0.2–0.4)	33 (0.2–0.4)			24	5	21	21	2	14
0.3–0.4									*	4	6	9		7
0.4–0.5				27 (0.4–0.6)	16 (0.4–0.6)	17 (0.4–0.6)				2	4	2		5
0.5–0.6										1	1	2		4
0.6–0.7				13 (0.6–0.8)	14 (0.6–0.8)	10 (0.6–0.8)					*	2		
0.7–0.8												2		
0.8–0.9					6 (0.8–1.0)	3 (0.8–1.0)						*		
0.9–1.0														

* Indicates percentage is less than 0.5%.
** Sampling level 0.0–0.3 m.
*** Sampling levels are 0.2 m thick.

TABLE 3. LEAF BIOMASS DISTRIBUTION, ROOT BIOMASS DENSITY, AND LEAF:STEM BIOMASS RATIOS IN DIFFERENT LEVELS ABOVE AND BELOW THE SOIL SURFACE. Measurements were not made on *A. fasciculatum* 2 and *C. odorifera*.

	Species and number of individual										
Height (m)	*Ceanothus greggii*		*Adenostoma fasciculatum**			*Heteromeles arbutifolia*	*Arctostaphylos glauca*	*Satureja gilliesii**			
	1	2	1	3	4	1	1	1	2	3	4
Root biomass density (g m^{-3})	**	**	**	***	***	**	**				
0.0–0.1				150	102						
0.1–0.2	740	290	400			3000	1370	362	412	265	220
0.2–0.3				72	92			215	325	88	138
0.3–0.4								182	46	108	121
0.4–0.5				53	47			2	30	29	54
0.5–0.6									18	22	12
0.6–0.7				46	28				1	6	12
0.7–0.8										1	12
0.8–0.9				20	7						1
0.9–1.0											
Leaf:stem biomass ratio											
1.6–1.8						6.14					
1.4–1.6						1.68					
1.2–1.4						0.50					
1.1–1.2	0.66					0.71	2.63				
1.0–1.0	1.00					0.28	3.04				
0.6–0.8	4.80	2.20				0.21	1.12				
0.4–0.6	0.03	1.68				0.05	0.50				
0.2–0.4	0.0	0.44				0.02	0.12				
0.0–0.2	0.0	0.06				0.0	0.03				

* Leaves were not separated from stems.
** Rooting level 0.0–0.3 m.
*** Rooting levels are 0.2 m.

TABLE 4. FRACTION OF THE TOTAL ROOT LENGTH IN DIFFERENT SOIL DEPTHS AND SIZE CLASSES. The mean total root length for four *Satureja* plants 49.2 m and for two *Colliguaya* plants 8.3 m.

Soil depth	Root diameter class (mm)							
(m)	0–0.5	0.5–1.0	1–2	2–4	4–6	6–8	8–10	> 10
				Satureja				
0–0.1	0.265	0.064	0.031	0.029	0.017	0.011	0.008	0.005
0.1–0.2	0.105	0.048	0.050	0.021	0.010	0.003	0	0
0.2–0.3	0.093	0.050	0.052	0.019	0.006	0	0	0
0.3–0.4	0.025	0.023	0.016	0.006	0.001	0	0	0
0.4–0.5	0.009	0.007	0.007	0.001	0	0	0	0
0.5–0.6	0.007	0.005	0.001	0	0	0	0	0
0.6–0.7	0.002	0.002	0.002	0	0	0	0	0
Total	0.506	0.199	0.159	0.076	0.034	0.014	0.008	0.005
				Colliguaya				
0–0.1	0.203	0.122	0.087	0.052	0.023	0.006	0	0
0.1–0.2	0.151	0.110	0.070	0.046	0	0	0	0
0.2–0.3	0.035	0.041	0.036	0	0	0	0	0
0.3–0.4	0.006	0.006	0.006	0	0	0	0	0
Total	0.395	0.279	0.199	0.098	0.023	0.006		

summer, so soil systems can be expected to be organized for the efficient uptake of these minerals. To absorb phosphorus efficiently a root system should have roots or mycorrhizae about 0.5 cm apart because of low mobility of phosphorus in the soil (Bieleski, 1973). For efficient absorption of nitrate, roots should be about 4 cm apart (Van Keulen et al., 1975) and for water, about 8 cm apart (Lambert and Penning de Vries, 1975). If a biomass of fine roots adequate to exploit the soil nitrate is added to our measured values, root:shoot ratios from 0.26 to 0.93 are calculated; to exploit the soil phosphate, root:shoot ratios from 0.34 to 3.35 are obtained. Ratios above 1.0 are always associated with rooting systems deeper than 0.5 m and small calculated root biomass densities. It is unrealistic to add the full biomass density to these sparse root systems, because the larger roots are not present to support the development of the fine roots. Thus, we conclude that the root-shoot ratios of chaparral shrubs, even though some are considered deep–rooted, have root: shoot ratios between 0.3 and 1.0 and have root biomasses concentrated near the soil surface.

ACKNOWLEDGMENTS

This work was supported by NSF grant DEB75–19491 as part of the IBP-Origin of Ecosystem Structures project. We thank Mr. Ernesto Hajek, Universidad Catolica de Chile, for his support in Chile and Dr. Jochen Kummerow and Mr. Wayne Stoner, San Diego State University, for their critical discussions and Ms. Martha Poole and Patsy Miller for their help in preparing the manuscript.

Literature Cited

Aschmann, H. 1973. Distribution and peculiarity of Mediterranean ecosystems, p. 11–19. *In* F. diCastri and H. A. Mooney (eds.) Mediterranean type ecosystems: Origin and structure. Springer-Verlag, New York.

————, and C. Bahre. 1977. Man's impact on the wild landscape. *In* H. A. Mooney (ed.) Convergent evolution in California and Chile. Dowden, Hutchinson, and Ross, Stroudsburg, Pa. (in press).

Bielski, R. L. 1973. Phosphate pools, phosphate transport, and phosphate availability. Ann. Rev. Plant Physiol. 24:225–252.

Caldwell, M. M. and O. A. Fernandez. 1975. Dynamics of Great Basin shrub root systems, p. 38–51. *In* N. F. Hadley (ed.) Environmental physiology of desert organisms. Dowden, Hutchinson, and Ross, Stroudsburg, Pa.

Christensen, N. L. and C. H. Muller. 1975. Effects of fire on factors controlling plant growth in *Adenostoma* chaparral. Ecol. Monogr. 45:29–55.

Dennis, J. G. and L. L. Tieszen. 1972. Seasonal course of dry matter and chlorophyll by species at Barrow, Alaska, p. 16–21. *In* S. Bowen (ed.) Proceedings 1972 Tundra Biome Symposium, Lake Wilderness Center, University of Washington, 3–5 April 1972. U.S. International Biological Program, U.S. Arctic Research Program, U.S. Tundra Biome, Hanover, New Hampshire.

Hellmers, H., J. S. Horton, G. Juhren, and J. O'Keefe. 1955. Root systems of some chaparral plants in southern California. Ecology 36:667–678.

Kummerow, J., D. Krause, and W. Jow. 1977. Root systems of chaparral shrubs. (pers. comm.).

Lambert, J. R. and F. W. T. Penning de Vries. 1975. Dynamics of water in the soil-plant-atmosphere system: A model named Troika, p. 257–273. *In* A. Hadas (ed.) Ecological Studies. Analysis and Synthesis, vol. 4. Springer-Verlag, Berlin.

Miller, P. C. and H. A. Mooney. 1974. The origin and structure of American arid-zone ecosystems. The producers: Interactions between environment, form and function, p. 201–209. *In* Proceedings First International Congress of Ecology, The Hague, Netherlands.

————, D. Bradbury, N. Thrower, V. La Marche, and E. Hajek. 1977. Macroclimate. *In* H. A. Mooney (ed.) Convergent evolution in California and Chile. Dowden, Hutchinson, and Ross, Stroudsburg, Pa. (in press).

Shachori, A., D. Rosenzweig, and A. Poljakoff-Mayber. 1967. Effect of Mediterranean vegetation on the moisture regime, p. 291–311. *In* W. E. Sopper and H. W. Lull (eds.) International Symposium on Forest Hydrology. Pergamon Press, New York.

Van Keulen, A., N. G. Seligman, and J. Goudrian. 1975. Availability of anions in the growth medium of roots of an actively growing plant. Neth. J. Agris. Sci. 23:131–138.